

Studies in Upside-down Flies (Diptera: Neurochaetidae) Part II. Biology, Adaptations, and specific mating Mechanisms

DAVID K. MCALPINE

McALPINE, D. K. Studies in upside-down flies (Diptera: Neurochaetidae). (Part II. Biology, adaptation, and specific mating mechanisms. *Proc. Linn. Soc. N.S.W.* 110 (1), (1987) 1988: 59-82.

Field observations and apparent host plants (families Araceae, Musaceae, Pandanaceae, and Zingiberaceae) are recorded for some species. Pollen-feeding is recorded for adult *Neurochaeta inversa*. Aspects of adult morphology and behaviour are considered in relation to adaptation, in particular to running (including running backwards), infrequent flight, living in crevices, adult longevity, specialization and reduction of options, ecological advantages of 'upside-down' behaviour, and diversity of male postabdominal morphology (including evolution of the protandrium). Male post-abdominal diversity in general is here placed in the category of *specific mating mechanisms*. This common but little understood concept is compared critically with the premating isolating mechanism concept and the specific mate recognition system concept. The legitimacy of seeking Darwinian explanations for morphological specializations is discussed.

David K. McAlpine, *The Australian Museum, Box A285 Sydney South, Australia 2000*; manuscript received 21 May 1986, accepted for publication 22 July 1987.

INTRODUCTION

Part I of this study (McAlpine, 1988) dealt with the systematics and phylogeny of the Neurochaetidae, including the genera *Neurochaeta*, *Nothoasteia* and the extinct *Anthoclusia*. Some information on biology, behaviour, and ecology of the Australian *Neurochaeta inversa* McAlpine has been given by McAlpine (1978), Shaw, Cantrell, and Houston (1982), and Shaw and Cantrell (1983).

Neurochaeta inversa and the East Malaysian *N. macalpinei* Woodley (1982) are both associated with the araceous plant *Alocasia macrorrhiza* (L.) G. Don. Apparent host plants belonging in other families are here recorded. These are all large monocotyledons, perhaps all providing some kind of phytotelma in which the larvae may be expected to live. It is probable that adaptation to the host microhabitat has influenced some of the morphological peculiarities and diversity of adult Neurochaetidae, but variation in other characters, particularly those of the male postabdomen, is paralleled in other dipterous families and may be a by-product of the speciation process.

FIELD OBSERVATIONS (WEST MALAYSIA)

Neurochaetids were observed by K. C. Khoo and the author in rain forest along the Old Bentong Pass road between Gombak village and Genting Highlands turnoff on 14-16 April 1985.

Adults of *Neurochaeta parviceps* were found in small numbers on peduncles of the club-shaped young inflorescences of wild ginger, *Zingiber spectabile* Griff. Several other species of ginger (Zingiberaceae) were flowering in the area, but no neurochaetids could be found on them. These flies moved in the characteristic upside-down mode of the genus (see McAlpine, 1978), very rapidly when pressed, and their elusive movements made them difficult to capture with an aspirator, though aspiration proved the most

effective method of capture. They sometimes sheltered in the small cavities of the stem bracts, but never in the floral bracts which were always brim-full of rain water. When disturbed they eventually ran, or more rarely flew, to other parts of the plant. If persistently pursued they sometimes left the plant altogether. A mating pair of *N. parviceps* was seen by Khoo on a *Zingiber* plant.

In this habitat some specimens of *Neurochaeta capilo* were also collected. These were consistently on the leaf blades and petioles of wild banana (*Musa* sp., Musaceae). A few specimens of *N. parviceps* also found on the banana were possibly recently disturbed from an adjacent ginger plant. Only certain plants of *Musa* in the areas appeared attractive to *N. capilo*, and there was evidence of repeated return of probably the same individual to such plants. One of these attractive plants supported numerous specimens of *Formicosepsis*, otherwise scarce in the area, and there was frequent non-aggressive contact between these and *Neurochaeta*.

OBSERVATIONS ON *NEUROCHAETA MAGNIFICA* IN PAPUA NEW GUINEA

J. W. Ismay reports as follows (*in litt.*): 'I was collecting at Mur Mur Pass in the Tomba Gap at approximately 143°59'E, 5°50'S [2760m]. . . . The area had been partly cleared but some young *Pandanus* were left. The *Neurochaeta* were seen on the inside of upright leaves of *Pandanus*, walking up and down with the head always downwards. They ranged to the tops of the leaves. The silver markings on the back of the head and behind the scutellum were conspicuous against their dark coloration. Some were caught by sweeping a net against the leaves, but most, when approached, ran down the leaf base and were pooted. They were at least as fast as *N. inversa*, which I have taken in Queensland.'

HOST PLANTS

All specimens of *Neurochaeta parviceps* were found on or near *Zingiber spectabile*. At the time only young inflorescences were present, none having reached anthesis. These young inflorescences terminate in a cluster of bracts, each of which remains full of rain-water, because of the almost daily rainfall and low evaporation rate. Several kinds of dipterous larvae were found in this liquid from three sampled inflorescences, but none of these could be identified as *Neurochaeta* from comparison with the known third-instar larva of *N. inversa*, though some very small, probably first-instar cyclorrhaphous larvae were found. I do not regard this as strong evidence that the larvae of *N. parviceps* do not live in the water trapped in the bracts of *Zingiber*; on the contrary I think that at a later stage of development this is most likely to be the larval habitat.

The sample of *N. parviceps* obtained by Khoo and me has the unexpected sex ratio of 31 males to 3 females. The biological significance of this is not apparent.

The strong attraction of adults of *Neurochaeta capilo* to plants of wild banana (*Musa* sp.) is established by observations recorded above. If this species is as closely associated with a host species in all stages as is *N. inversa*, then *Musa* would seem to be the larval host, but those plants on which the flies were found had closely appressed petiole bases, leaving no axillary cavities, and no inflorescences. At the time the adults were collected, only a very small percentage of *Musa* plants had inflorescences and these appeared to have no actual or potential water-holding parts. *Musa* plants are, however, often reported to provide phytotelmata.

The identity of the *Pandanus* host of *Neurochaeta magnifica* is uncertain. Ismay was informed by a villager that the plants were 'karuka', a name used in Papua New Guinea to designate *Pandanus* spp. useful for production of thatching and matting, and also for their edible fruits. In highland areas of Papua New Guinea, *Pandanus julianettii* and *P.*

brosimos are the principal 'karuka' species and their fruits are an important local food source (Stone, 1982). *P. brosimos* occurs in the Tomba vicinity close to the type locality of *Neurochaeta magnifica* (Stone, 1982: figs 6, 7) and may be the host of this fly, but this is only one of about 66 species of *Pandanus* known from New Guinea.

Stone also states: 'The pandan leaf axil is of considerable interest. It is usually stocked by the infall of detritus from above, usually retains water to the extent of a cupful or more, or a thick solution of decaying debris, and may incorporate dying fragments of the endo-axillary rootlet system.' Among the invertebrates living in this habitat he mentions larvae of cyclorrhaphous flies. Thus this appears to be a likely habitat for the larvae of *Neurochaeta magnifica*. However, Ismay (*in litt.*) points out: 'Since the [karuka] palms are 10-30m high and very spiny, few entomologists collect from them. Also, they cannot be tampered with — damage to karuka is a common cause of tribal conflict in the Highlands'.

FEEDING IN *NEUROCHAETA INVERSA*

At Mount Tenison Woods, D'Aguilar Range, near Brisbane, Queensland, on 4.ii.1983, K. C. Khoo and I observed inflorescences of *Alocasia macrorrhiza* being visited by three species of insects, all taking pollen from the spadix. These were *Neurochaeta inversa*, *Trigona* sp. (apparently *T. carbonaria* Smith, det. E. Exley, a native social bee) and *Apis mellifera* L. The last species was in the smallest numbers, but tended to disturb or disperse the others when present. Clearly, higher concentrations of *A. mellifera* would have inhibited seriously the activities of the other two species.

We observed numbers of *N. inversa* adults repeatedly licking the surface of the male section of the spadix and apparently ingesting pollen. On a number of occasions the flies were seen to approach the hind leg of a *Trigona* and actively lick at the pollen load. The *Trigona*, in each case, attempted to withdraw its leg or move away, but the fly often followed to some extent.

While *Alocasia* pollen provides a high protein food source for *N. inversa*, this food is available only during the summer flowering period of the plant. My previous conjecture, that the flies feed on various substances collected on the large leaves of *Alocasia*, is supported by further observations (Border Ranges National Park, near Kyogle, N.S.W., 3.iv.1987). Periods of running activity on leaf surfaces were interrupted at intervals when the flies began licking at spots of unidentified substances on the leaf surface. When drops of diluted orange-marmalade were smeared in their paths, the flies stopped to feed on it. Thus the leaf-surface activity is to be interpreted as foraging.

LOCOMOTION AND LEG STRUCTURE

I have described for *N. inversa* (McAlpine, 1978) the habit of running rapidly backwards and forwards with constant head-downwards orientation while on a vertical surface. This habit is now also recorded for a further four species of the subgenus *Neurochaeta*, viz. *N. parviceps* and *N. capilo* (observations by K. C. Khoo and author), *N. macalpinei* (observations reported to author by J. Frazier and D. Clyne, noted Woodley, 1982), and *N. magnifica* (Ismay's observations). Almost certainly the fifth species of the subgenus, *N. sabroskyi*, has the same habit.

The speed and the erratic nature of running are remarkable in subgenus *Neurochaeta* for such small insects. I have observed a specimen of *N. inversa* to run at an average speed of about 3.7cm/sec for a period of 30sec, during which time the direction of movement was reversed about 50 times. Under similar conditions an active specimen of *Stenomicroa* sp. of similar size moved at about 1.2cm/sec with only about 6 fairly abrupt reversals of direction in 30sec.

The specialized running mechanism of *Neurochaeta* appears to have certain advantages in: (1) avoiding predators, (2) finding scarce food substances by covering a large area of plant surface in a short time, (3) seeking out small apertures (e.g. for escape from plant cavities), (4) the searching out of conspecific individuals in aggregation and perhaps in sexual activity.

Differentiation of the leg proportions is characteristic of the family. These are particularly expressed in the relative size of the femora and the general description is as follows: fore femur short and stout; mid femur short and slender; hind femur long and moderately stout; tibia of each leg shorter than femur. The precise proportions of the femora vary between the species as shown in Table 1. The fossil *Anthoclusia gephyrea* has the least differentiation in femoral length, according to the scale drawings of Hennig (1965: figs 251, 252), and this appears to be the most plesiomorphic condition known in the family. *Neurochaeta magnifica* and the species of *Nothoasteia*, on the other hand, have the greatest differentiation. The reduction of the mid legs in *Nothoasteia* is reminiscent of that of wingless males of the hymenopterous family Agaonidae.

It seems logical to relate the unusual leg proportions of neurochaetid flies to the mode of locomotion which is characteristic of all observed species, even though present knowledge does not explain the mechanistic aspects of this relationship.

TABLE 1

Relative lengths of femora in neurochaetids
Ratios fore femur: mid femur: hind femur

<i>A. gephyrea</i>	♂. 1: 1.1: 1.4	♀. -
<i>Ne. capilo</i>	♂. 1: 1.2: 1.8	♀. 1: 1.2: c.1.9
<i>Ne. inversa</i>	♂. 1: 1.1: 1.9	♀. 1: 1.1: 1.9
<i>Ne. magnifica</i>	♂. 1: 1.2: 2.7	♀. 1: 1.2: 2.6
<i>Ne. sabroskyi</i>	♂. -	♀. 1: 1.0: 1.9
<i>Ne. parviceps</i>	♂. 1: 1.1: 1.9	♀. 1: 1.0: 1.9
<i>Ne. macalpinei</i>	♂. 1: 1.0: 1.8	♀. 1: 1.0: 1.8
<i>No. clausa</i>	♂. -	♀. 1: 0.7: 2.1
<i>No. platycephala</i>	? 1: 0.8: 1.9	

Flies of the genus *Nothoasteia* are remarkable and perhaps unique among the Schizophora in the absence of anything in the nature of a tarsal claw. Because tarsal claws are so generally present in Diptera, it is certain that they fulfil a function in their biology which cannot normally be dispensed with. Presumably the primary function is clinging to surfaces, which are either rough or sufficiently soft for an impression to be made by the sharp claw apex. One might, then, infer that *Nothoasteia* normally lives on surfaces which offer no such opportunity for gripping with claws, such as a hard, smooth surface or a loose powdery one. The paired pulvilli are well developed on all tarsi of *Nothoasteia*, as in other neurochaetids. These are pads of sticky hairs which enable most flies to cling to and walk on smooth surfaces, even if the surface is vertical or facing downwards (e.g. a window pane or ceiling). They do not function on wet surfaces (so far as known). If non-sticky, these pads could aid walking on a powdery surface.

While absence of functional claws may seem to set *Nothoasteia* apart from the rest of the Neurochaetidae, there is variation in claw size between species of the subgenus *Neurochaeta*. Also there may be variation in claw size in the one individual, those of the smaller mid legs often being slightly smaller than those of the large hind legs. *Neurochaeta capilo* and *N. parviceps* are flies of similar size, but the hind tarsal claws of the former are at least twice as long as those of the latter species. The other species of the *parviceps* group

have claws of similar proportions to those of *N. parviceps*, but *N. inversa* has claws intermediate in size between those of the *capilo* and *parviceps* groups.

The strong, moderate-sized claws of *Neurochaeta inversa* are similar to those of periscelidids and many other small acalyptrate flies, and probably approximate to the plesiomorphic condition for the *Neurochaetidae*. The elongate, needle-like condition in *N. capilo* and the shortened condition of the claws in the *parviceps* group appear to be apomorphies which have developed in opposite directions. Claw reduction in *Nothoasteia* is clearly independent of and convergent with that in the *parviceps* group. The adaptational significance of this reduction may become clearer when studies are made of living *Nothoasteia*.

RUNNING BACKWARDS

The orientation of the hairs and bristles on the dorsal surface of flies with apices directed posteriorly is apparently an adaptation to walking (and probably to flying) forwards with minimal resistance. Though several (perhaps all) species of *Neurochaeta* walk backwards as much as they walk forwards (and probably for much longer periods than they fly forwards), the orientation of most hairs and bristles remains as in strictly forward-walking flies, though a few of the dorsal bristles are sometimes nearly erect. These longer bristles would tend to shield the posterior mesoscutal hairs from contacting any obstacle dorsal to the insect. By contrast the hairs on the median region of the posterior half of the mesoscutum in *Nothoasteia clausa* are directed forwards, those on the anterior part being largely directed backwards; most bristles are quite short and there are no long posteriorly directed ones. In the absence of behavioural records of this rare fly, this condition suggests that the backward locomotion may be at least as important as forward locomotion in *Nothoasteia*. The legs of *Nothoasteia* are similar to those of some apomorphic types found in *Neurochaeta*, e.g. in *N. parviceps*, particularly in the long hind femora and reduction in size of the mid legs; also the body-form is strongly depressed, and reduction of the prosternal plate has extended to complete loss. These features suggest behavioural similarity in the two groups. Because *Nothoasteia* has not acquired apomorphic wing-venational characters present in the groundplan of subgenus *Neurochaeta*, it is evident that the extreme developments of the legs and body-form have been acquired independently in the two groups. As the developments are mostly present in a less elaborated state in such plesiomorphic neurochaetids as *Anthoclusia* and subgenus *Neurocytta*, it is not surprising that similar states of elaboration should have been achieved in different lineages.

Concentration of organs of vision on the anterior end in insects is an obvious adaptation to forward locomotion, perhaps particularly to forward flight as non-flying cursorial insects (e.g. worker ants) generally have reduced eyes. Because, in subgenus *Neurochaeta*, running backwards is a more frequent occupation than forward flight, one might expect some modification of vision in connection with this behaviour.

In all the species of the genus *Neurochaeta* the eyes are obliquely elongate. Thus, though total area of the eye is not great, there is a larger number of ommatidia facing dorsally than in other cursorial flies (such as phorids, and certain sphaerocerids). In living examples of *N. inversa* and *N. parviceps*, there is a characteristic concave-backed profile resulting from the head being held away from the substrate through dorsal flexion at the neck. This unusual position contrasts with that of dried specimens, and careful examination shows that several ommatidia would then provide some vision in a posterior to posterodorsal direction. The convex posterior extremity of the eye in *N. magnifica* could also increase posterior vision.

Previously (McAlpine, 1983) I recorded observations indicating that the aulacigastriid flies *Nemo centriseta* McAlpine and *Nemo kentae* McAlpine walk consistently forward, while *N. corticeus* McAlpine and *N. phaeotylus* McAlpine often walk backwards and forwards with abrupt reversals of direction at short intervals. I have recently examined the eyes of these four species, and find that the posterodorsal margin of the eye in the two latter species is extended slightly further on to the posterior surface of the head and has the marginal ommatidia directed slightly more in a posterior direction than in the former pair of species. Firm conclusions as to this apparent connection between behaviour and structure require more observations on *Nemo* spp. than those yet made. Except for *N. centriseta*, the observations have been few, and the morphological difference between the two species pairs is small. However, if such a connection is proved for *Nemo*, this would strengthen the expectation of comparable adaptations in *Neurochaeta*, where backward motion is a more significant element of behaviour.

In neurochaetids the parts projecting furthest posteriorly, and therefore those which usually make first contact with an obstacle in running backwards, are the wing tips and the tip of the abdomen. In the subgenus *Neurochaeta* and in *Nothoasteia* the wing tips have special hairs or setulae which could be tactile. In the former they form a small, compact group at the apex of vein 3; in *Nothoasteia* these setulae are not in such a compact group, and the short section of the costa bearing them, between veins 3 and 4, is remarkably thickened. This thickening could be a strengthening device in a part subject to battering when the insect runs backwards.

In most species of the subgenus *Neurochaeta* the cerci of both sexes are broadened, exerted, and fringed with long setulae. The possibility of these structures acting as tactile organs and buffers for running backwards could explain why the cerci, which usually have evolved along different lines in each sex, have here evolved the same apomorphic condition in both sexes. *N. capilo* is the only species of the subgenus *Neurochaeta* with cerci short (in female) or not posteriorly prominent (in male), although it is capable of running backwards at speed. This species is apparently a sister group to the rest of the subgenus, and has probably never acquired these apparently adaptive attributes, despite an equally long history of running backwards. This condition of the cerci is perhaps explained by the insect having larger wings, a further plesiomorphic character.

Nothoasteia also lacks modifications of the cerci or other apical abdominal parts. In *Neurochaeta capilo* and *Nothoasteia* the greater size of the wings relative to the abdomen renders it less probable that the abdomen would make first contact with an obstacle. Perhaps also *N. capilo* lives in a more open habitat than *N. inversa*, *N. parviceps*, and *N. macalpinei*, and is thus less likely to run into objects.

Examples of adaptation for running backwards as well as forwards in other animals seem to occur mainly in types living in tunnels or burrows, where it can be advantageous to reverse direction of locomotion without turning the body. Moles of the genus *Talpa* (Mammalia: Insectivora) are reported to run as fast backwards as forwards (Boon-song and McNeely, 1977). The fur of moles is soft and velvety, and can lie in any direction, enabling the animals to go backwards and forwards in a burrow without the grain of the fur giving resistance. These facts prompt comparison with *Nothoasteia* and raise the questions: Does *Nothoasteia* live in tunnels or burrows? Can its dorsal thoracic setulae have their direction reversed, like moles' fur, or is their position, as described above, permanent? In *Talpa micrura* Hodgson the tail is much reduced, but acts as a sensory organ when it is running backwards. This compares with the posterior sensory organs of *Nothoasteia* and subgenus *Neurochaeta*.

FAST FORWARD LOCOMOTION

In view of the presence of apparent adaptations for rapid backward movement, comparable adaptations for forward movement in neurochaetids should also be considered, as forward running appears to be just as frequent and rapid as backward running. As mentioned above, forward vision is well developed. Forwardly directed vibrissae are present in *Neurochaeta*, but the anterior parts most liable to the effects of collision are the antennae. Antennal segment 3 is presumably furnished with the usual complex and delicate array of sense organs found in higher Diptera, including chemoreceptors. The rather long hairs on the anterior surface of this segment would afford some protection to these organs in *Neurochaeta*, and segment 3 is particularly well protected from physical contact with surrounding objects by the large, cucullate segment 2, which, in subgenus *Neurochaeta*, bears strong anterior bristles. The arista projects further forwards than other parts of the antenna and could serve to sense an imminent collision rather than to shield physically other parts from contact.

In species of subgenus *Neurochaeta*, which, so far as known, tend to flex the head upwards, the anteriorly inclined median ocellus would be unable to receive stimulation from a light source directly in front of the insect, were it not for the fact that the postfrons has a median channel leading to the space between the antennae. In some species, e.g. *N. magnifica* and *N. parviceps* it is scarcely wider than the ocellus, very well defined, and commences immediately in front of the ocellus.

INFREQUENT FLIGHT

Observations on species of the subgenus *Neurochaeta* seem to indicate that running is a more frequently used escape mechanism than flying and that flight is an infrequently used form of locomotion. Nevertheless all species for which we have field observations can fly (i.e. all species except *N. sabroskyi*), and flight is probably necessary for dispersal to new host plants. *N. macalpinei* shows reduction of the wing area, which is probably an indication of the lesser importance of flight in its biology. Comparison of the wings in *N. macalpinei* and *N. parviceps* suggest that the latter also has undergone slight reduction of the wing and that the loss of the free distal part of vein 5 is an element of this reduction (also occurring in a third species, *N. sabroskyi*, with slightly longer but narrower wing). *N. parviceps* often seemed most reluctant to fly in the field, probably more so than *N. capilo* which lacks these indications of wing-reduction (though field observations on the latter species were restricted to few individuals).

N. macalpinei not only shows the greatest wing reduction of any known *Neurochaeta* species, but also the most marked shortening of many of the bristles, notably the fronto-orbitals, dorsocentrals, and scutellars, though the notopleurals are quite long. There seems a possibility that the bristle-shortening is an adaptation to infrequent flight, though the importance of bristles in flight is not well understood. On the other hand *Nothosteia* species show a much greater bristle reduction without apparent reduction of wing area. This is not just a reduction in length, but an overall reduction in size and number of the bristles, and, in parts, also a reduction of the hairs. The case of *Neurochaeta macalpinei* is reminiscent of the genera *Baeopterus* (Coelopidae) and *Calycopteryx* (Micropezidae), both flightless examples with shortened bristles in families of normally actively flying forms.

LIVING IN CREVICES

I have already concluded (McAlpine, 1978) that in *Neurochaeta inversa* the dorso-ventrally compressed body is an adaptation to moving through narrow spaces, such as are provided by the host plant, *Alocasia*. This ability has been confirmed on two

occasions when several adults of *N. inversa* escaped from a collecting jar by way of the thread of the screw-top, which had an imperfect inner seal. By comparison, *N. capilo* is much less depressed. Perhaps, if *Musa* is the only host of this species, then there is less necessity and opportunity for creeping into narrow spaces. One individual, apparently of *N. capilo*, when pursued, was seen to shelter in the channel on the adaxial side of the banana petiole, but this was a relatively open and capacious hollow.

Neurochaeta parviceps has a more strongly depressed body than other *Neurochaeta* species which I have observed in the field, though in *N. macalpinei* it is almost as depressed and in *N. magnifica* more so. *N. parviceps* has been seen to shelter in the narrow and shallow spaces in the axils of the bracts on the peduncles of young inflorescences of *Zingiber spectabile*. A reduced depth of the thoracic region by comparison with *N. inversa* is partly achieved through reduction in size of the mid coxae and their migration from near the median line to a more lateral position on the thorax. This results in a greater ventral exposure of the metasternum (which in *N. inversa* tends to be concealed by the mid trochanters). In the *parviceps* and *magnifica* groups the ventrally directed anterior sterno-pleural bristles and the setulae on the metasternum are particularly well developed, in response, I believe, to the need for feeling the substrate in an insect in which the thorax is held unusually close to it.

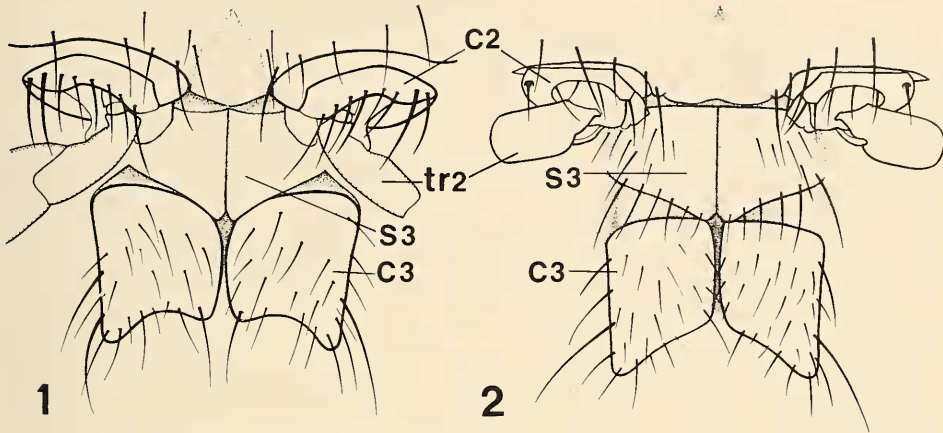
The thoracic pleura of *N. parviceps* and to some extent those of related species (including *N. inversa*) have, laterally to the fore coxa, a marked ventrally facing hollow, which appears to enable relatively free movement of the laterally splayed fore legs, without their occupying space between the thorax and the substrate.

The size and apparent resting position of the fore coxa, as evidenced from dried material, varies among species of Neurochaetidae, and these attributes relate to the variations in structure of the prothoracic furcasternum. In *Neurochaeta capilo* the furcasternum is not prominent and is covered by the more or less distally contiguous, bulky fore coxae. The coxae appear to work largely below the sternal region of the thorax, occupying a significant part of the depth of the insect. In *N. parviceps* the broad, flat furcasternum rather widely separates the more laterally placed fore coxae. The coxae are less bulky than in *N. capilo*, compressed, keeled, and apparently adapted for movement within the pleural hollow without occupying much space below the thorax. In *N. inversa* the condition is intermediate between that of *N. capilo* and *N. parviceps*. The furcasternum is rather narrowly convex and the coxae, though decidedly separated at rest, are generally less so than in *N. parviceps*. The condition in *N. macalpinei* and *N. sabroskyi* is similar to that of *N. parviceps*, but in the former the rather small coxae are neither compressed nor keeled.

In *Neurochaeta magnifica* the structure and co-adaptation of these prothoracic parts are quite different from the above types. The problem of the working of the forelegs under a remarkably shallow thorax has been solved by a migration of the coxa almost to the lateral extremity of the thorax, the section of the pleura above it being almost vertical and exceedingly shallow to accommodate the coxa. With the fore coxae extremely distant from each other and the prothoracic pleura quite limited to the lateral surfaces of the thorax, there remains a ventral prothoracic surface much broader and more open than in other species. The furcasternum is thus even broader than in *N. parviceps*, and the very broad prosternal plate is unlike that of any other neurochaetid.

In *Nothoasteia clausa* the condition of the fore coxae most resembles that of *Neurochaeta macalpinei*, but there is no pleural hollow.

In contrast to the mid coxa, mobility of the fore coxa is essential to the operation of the leg in locomotion; hence the quite different nature of its specialization.



Figs 1, 2. Metasternum and surrounding parts of *Neurochaeta* spp. 1. *N. inversa*. 2. *N. parviceps*. c2 = mid coxa. c3 = hind coxa. s3 = metasternum. tr2 = mid trochanter

The erect dorsal bristles on the wing and scutellum in the subgenus *Neurochaeta* are probably important tactile organs when the insect moves under a low ceiling. There is a similarity here to suberect apical scutellar bristles of the genus *Nemo* (family Aulacigastriidae, see McAlpine, 1983). At least some species of *Nemo* shelter under bark, a habitat which provides a low ceiling.

The plant association is unknown for *Neurochaeta sabroskyi*, but its proportions suggest a slightly different direction of specialization from that of related species. It seems probable that it is a sister species to *N. parviceps*, and out-group comparison both for the species pair and the collective group tends to confirm its derivation from broadly depressed forms. Yet *N. sabroskyi* has a much more slender body and wings. Although the fore coxae somewhat resemble those of *N. parviceps*, the pleural hollow is less marked, because narrowing of the mesoscutum allows less overhang of the pleural region. Hence we appear to have an adaptation pattern which has moved from wide, shallow crevices to something like pin-holes, or, more probably, when the accommodation of the legs is considered, in grooves which are both narrow and shallow.

APPEARANCE AND POSSIBLE MIMICRY

On exhibiting living material of *Neurochaeta* to laymen, a typical comment is something like: 'Are they flies? They look more like ants'. This reaction is presumably the result of several visible features. The size and slenderness of these insects are likely to be attributed to certain familiar domestic ants (e.g. species of genera *Iridomyrmex* and *Techonormyx*) rather than to such familiar flies as domestic calliphorids and muscids. These attributes are, however, typical of numerous flies of the superfamily Asteioidea (in which Neurochaetidae are currently placed), and alone cannot be considered as evidence for mimicry of small ants by these flies. I shall consider some other characters which appear to support the view that some neurochaetids are Batesian mimics of small dolichoderine ants.

Adults of *Neurochaeta parviceps* and *N. inversa* have a general blackish body coloration relieved by a paler zone at the anterior end of the abdomen. The idea that this coloration may be of some adaptive significance receives support from the fact that it is emphasized by the pale sub-basal zone of the wings, when they are flexed over the abdomen, and also by the coloration of the halteres.

In *N. parviceps* and *N. inversa* in the subgenus *Neurochaeta* the halteres are bicoloured, with pedicels brownish and capitella creamy white. With the haltere directed posteriorly in the resting position, the dark pedicel lies against the dark posterior part of the thorax, and the whitish capitellum lies against the pale base of the abdomen. The wings being translucent, the coloration of the haltere reinforces the insect's longitudinal sequence of colour zones.

The coincidence of the distal parts of both wings over the abdomen gives the wings a low degree of visibility. The total impression, then, is of a slender, dark, wingless insect with a posterior part or gaster somewhat separated from the rest of the body, i.e. the appearance of a dark-coloured dolichoderine worker ant about 3 mm in length.

Comparison of *Neurochaeta* species with temperate Australian species of the micropezid genus *Metopochetus* tends to convince me that wing pattern in both is an element of Batesian mimicry of ants. *Metopochetus* species of the taxonomically unelucidated *M. terminalis* (Walker) complex are almost certainly mimics of ants of the genus *Leptomyrmex* (see Colless and McAlpine, 1970: fig. 34.29A, where incorrectly given as *M. tenuipes*). The larger *Metopochetus compressus* (Walker) is probably a mimic of aggressive stinging ants of the genus *Myrmecia*. These micropezid species have a complex wing pattern reinforced by superposition of the wings over the abdomen when at rest. The wings thus visually tend to lose their identity and give the impression of a basally narrowed, segmented abdomen. A closely related undescribed species of *Metopochetus* from Lord Howe Island has no wing pigmentation. Apparently there are no suitable ants to serve as models on this oceanic island. Several other micropezids, e.g. *Mimegralla contingens* (Walker) in northern Australia, New Guinea etc. and *Taeniaptera* spp. in Brazil, have a wing pattern similar to that of *Metopochetus* spp., though not closely related. Again I believe this convergence in pattern is best explained as due to ant-mimicry.

Neurochaeta species (e.g. *N. inversa*, see McAlpine, 1978: fig. 3) have a simpler wing pattern than the ant-mimicking *Metopochetus* species, probably because the smaller size of the former renders detailed representation of abdominal segmentation unnecessary.

Whether or not one is convinced of my theory of ant mimicry by *Neurochaeta* species, the evidence that colour pattern in these insects is adaptive is strongly supported by the fact that colour pattern of different parts of the insect is co-ordinated not only in such species as *Neurochaeta parviceps* and *N. inversa* as explained above, but also in other species with different schemes of coloration. *N. sabroskyi* has the capitellum of the haltere tawny, unlike other species of the genus, and also an almost uniformly brown-tinged wing membrane, and the anterior abdominal tergites brownish. *N. macalpinei*, on the other hand, has larger pale areas on the body than other species, paler legs, paler bristles, entirely creamy white halteres, and a larger pale sub-basal wing zone. The co-ordination of colour in wing, haltere and abdomen is apparent, and there is a possibility (but at present no evidence) that this species is a mimic of a small pale-coloured ant. In collecting the type series of *N. macalpinei*, Clyne and Frazier obtained, in association with the flies, a bug of the heteropterous family Anthocoridae. This is of similar size and coloration to the flies and could be a mimic of the same ant mimicked by them or even a mimic of the flies themselves. There is also a possibility that it is a predator of *Neurochaeta*.

The zigzag movements of *Neurochaeta* spp. are not particularly ant-like, though ants often do run quickly. This movement could, however, serve to display and reinforce the ant-like signal already learned by the predator.

A further feature observed in *Neurochaeta parviceps* and *N. inversa*, which is unusual for the higher Diptera and which increases resemblance to an ant, is the prognathous position of the head due to dorsal flexion at the neck in the living insect. The apparently short, high head of dried material is not ant-like, by comparison. The upward tilting of

the head has been interpreted above as possibly aiding vision in a posterior direction, but I see no reason why it may not also aid in protective mimicry.

Ants, including small dolichoderines, have relatively long conspicuous antennae. Neurochaetids have not been observed to compensate visually for this lack by an appropriate position or motion of the fore legs, as has been observed in a number of dipterous mimics of Hymenoptera (McAlpine, 1973: 9-10). On the other hand, general impression rather than precision of detail is probably more important in mimics of such small size.

Mimicry of ants by other insects and spiders is a common and well established phenomenon (Wickler, 1968; author's numerous observations, and numerous other references in literature). It has occasionally been doubted that ants are suitable models for Batesian mimicry because they are preyed upon heavily by insectivorous vertebrates, the predators through which visual selection is most likely to operate. On the other hand I believe it probable that ants which contain acrid chemicals are likely to bring about predator satiation at relatively low levels of predation, at least in non-specialist predators. The fact that ant numbers are often very large increases both the probability of predator satiation and the probability that the predator will learn the visual signal. Ants with such a powerful sting as *Myrmecia* naturally produce a cautious approach in an experienced predator, which is likely to increase the chance of escape for a mimic.

It is interesting to note that the Baltic amber fossil neurochaetid *Anthoclusia gephyrea* Hennig (1965: fig. 244) has a wing pattern somewhat resembling that of *Neurochaeta inversa*. This suggests the possibility that neurochaetids have been mimics of ants for as long as 40 million years.

ADULT LONGEVITY

From what is known of the life-cycle of *Neurochaeta inversa* in New South Wales, overwintering female adults would need to live for about 6 months in order to find an oviposition site and may in fact live even longer. Overwintering males seem to live about as long as females, from my observations, and mating appears not to take place till an oviposition site is available (see McAlpine, 1978). Though I am not aware of any longevity experiments for such small flies in the field, it is probable that *N. inversa* adults have rather exceptional longevity for their size class. Perhaps such behavioural peculiarities as the extreme agility in running, the tendency to seek shelter, the devices which protect the wings from battering, the infrequent use of flight, and ingestion of such protein-rich food as pollen are adaptations to prolonged survival. It would be interesting to compare longevity, behaviour, and relation to the seasonal cycles of the host plants of the equatorial Malaysian species with those of *N. inversa*.

SPECIALIZATION AND REDUCTION OF OPTIONS

As usual in cases of extreme specialization, the locomotory behaviour in *Neurochaeta* seems to have narrowed the range of biological options. Thus fast running is carried out almost exclusively with a strong forward or backward component, and, for reasons still unexplained, the insect is unable to remain in any position except that with the body axis vertical while on a vertical surface. It is possible that even this restriction on orientation is adaptive, as discussed below.

The elongate body in *N. inversa* appears to be remarkably rigid. When the insect feeds from a leaf surface, the head is not flexed from the neck, but the body remains straight as its anterior end is sloped towards the substrate.

Observation on a captive specimen of *N. parviceps* indicated a restriction in locomotion due to rigidity of the body. The insect was placed in a stoppered cylindrical glass

specimen tube c. 25mm by 50mm. The tube was inverted to give the container a glass ceiling. As expected, the insect ran up and down on the vertical glass wall with the body vertical and the head downwards. It repeatedly ran against the glass ceiling but each time it ran down again after contact. It was apparently unable to cross over the junction of the two surfaces at right angles to one another, and was reluctant to turn the body to make this transition possible. Eventually, after much contact with the ceiling, the body was turned horizontally and the transition to the ceiling readily made by walking sideways. Clearly inability to bend the body adequately, perhaps combined with shortness of the mid legs, prevented passing from the vertical to the horizontal surface when starting from the normal vertical body-position. No such difficulty existed for the insect in passing back from the ceiling to the wall, because, on the horizontal ceiling, there was no tendency towards a constant orientation of the body which could have prevented it approaching side-on to the vertical wall.

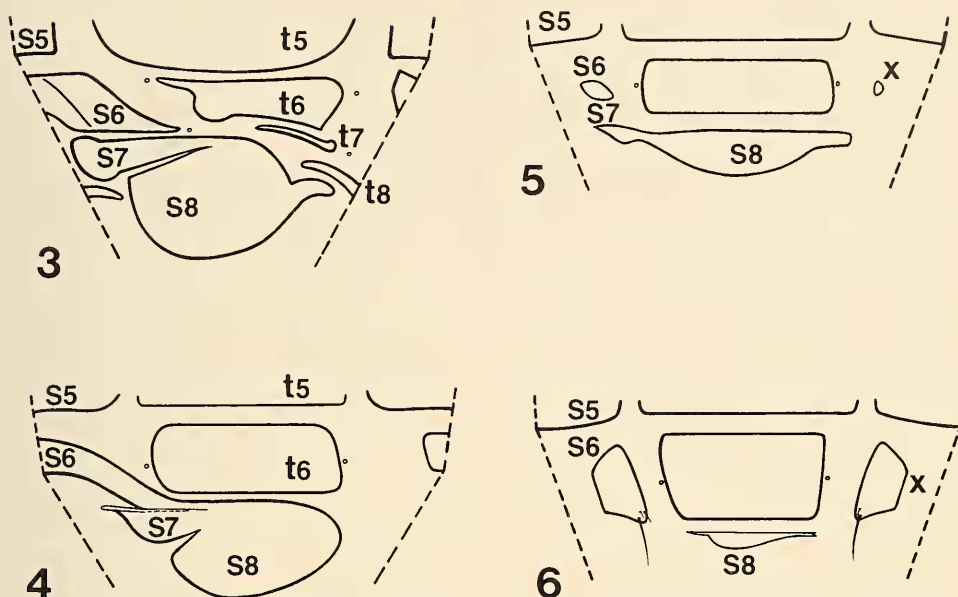
It is doubtful if the artificial situation just described simulates any frequently encountered natural situation. Flies on more mature inflorescences than those observed by us would frequently encounter the almost horizontal upper margins of bracts, and passing over this margin directly from the outer to the inner surface could pose a problem similar to that just described. One would expect, however, that any frequent, naturally occurring situation would not provide such difficulties in problem-solving. Field observations of *N. parviceps* in these situations would be interesting.

WHY UPSIDE-DOWN?

Given the advantages which may be conferred by the habit of running rapidly backwards and forwards in zigzags, the question remains as to why this habit has evolved in association with a head-down instead of an unrestricted or head-up orientation of the body.

It has been noted above that *Neurochaeta* species (and also *Nothoasteia* species) show apparent adaptations for running backwards, that these modifications are not uniform throughout the Neurochaetidae, and that the neurochaetid body-plan, like that of other Diptera, is primarily adapted for forward movement. In particular the eyes and other important sense-organs, which provide information as to conditions likely to be encountered during locomotion, are located on the head. It seems advantageous, then, for the neurochaetid fly to orient itself with the head pointing in the direction in which obstacles or dangers are most likely to be found. The cavities in which these flies shelter, e.g. the axils of bracts and hollowed petioles, and the spathal cavity of *Alocasia*, all open upwards, their closed lower ends forming an obstacle which, on repeated contact would eventually damage the wings. In the special case of phytotelmata, the opening is always upwards, and it would seem safest to approach the liquid surface, a potential sticky trap, head first. I have often noticed how moisture drops in glass vials tend to trap small flies by the wings. Thus, running wings-first towards the liquid surface could be particularly dangerous.

Some likely predators of *Neurochaeta* such as scincid lizards and frogs shelter in plant axils. Therefore running downwards into an axil head-first would seem more advantageous for flies than the reverse. Facing downwards while resting within the cavity does not, however, seem an advantageous position for watching for predators, and the neurochaetid habit of emerging from shelter backwards seems incautious. There is, however, a degree of rear vision and emerging backwards may not be particularly risky. The running is likely to be rapid and, as usual, evasive during emergence. A predator would need to be watching a particular axil carefully to be able to take advantage of a backward emergence.



Figs 3-6. Protandrograms of schizophorous Diptera, showing segments in front of male genital segment as if split along median ventral line and spread flat. 3. *Coelopa frigida* (Fabricius). 4. *Neurochaeta prisca* (reconstructed from notes and sketches). 5. *N. capila*. 6. *N. magnifica*. s5-s8 = sternites 5-8. t5-t8 = tergites 5-8. x = supernumerary sclerite.

It is interesting to note that flies of the genus *Stenomicroa* (family Perisclididae or Stenomicroidae), which often share the habitat of *Neurochaeta* species and are probably also associated with phytotelmata, maintain a consistent head-upwards orientation. But *Stenomicroa* are not known to shelter in axils, they run less rapidly than the observed *Neurochaeta* species, and they do not move backwards and forwards in a zigzag path (McAlpine, 1978).

I postulate that the head-downwards orientation in the Neurochaetidae evolved during the early stages of development of zigzag running. In view of apparent adaptations for running backwards in *Nothoasteia*, this kind of orientation may be expected to occur in all known living neurochaetids, and possibly occurred in the forms known from fossils. But it is conceivable that this orientation did not become rigidly stereotyped, as in the subgenus *Neurochaeta*, until the flies acquired habitat preferences which brought them into frequent contact with phytotelmata.

DIVERSITY IN MALE POSTABDOMINAL STRUCTURES

The few known species of the genus *Neurochaeta* show a great diversity of structure in the segments behind segment 5 of the male abdomen. The male is unknown in subgenus *Neurotexis*.

Variation in sternites 6-8 consists of degree of reduction of these sclerites. Sternites 6 and 7 are well developed in *Neurochaeta* (*Neurocytta*) *prisca* (Fig. 4), where they are strongly asymmetrically placed. In this form the dorsal sternite 8 is also well developed. Subgenus *Neurocytta* thus has the most plesiomorphic condition of these sternites known in the genus, as may be seen from the resemblance to the primitive schizophoran *Coelopa* (Fig. 3).

The remaining known species of the genus (subgenus *Neurochaeta*) show a trend towards reduction of sternites 6-8 and towards symmetry of these segments. *N. capilo* (Fig. 5) has sternites 6 and 7 much reduced but still discernible on the left side, while sternite 8 remains large and setulose. *N. macalpinei* and *N. parviceps* have these segments externally approximately symmetrical with a small sclerite below *each* lateral margin of tergite 6, and sternite 8 reduced to a narrow glabrous transverse strip. *N. inversa* resembles the above species in the symmetry of segment 6 but sternite 8 is absent. I previously (McAlpine, 1978) interpreted a dorsal sclerite of *N. inversa* as probably sternite 8, but comparison with other species of the subgenus not then available, indicates that the sclerite in question is the epandrium.

The protandrial structure of *Neurochaeta magnifica* is of special interest, most of its characters being strongly apomorphic. In contrast with that of other species of subgenus *Neurochaeta*, tergite 6, though unreduced, is asymmetrical, as is the reduced sternite 8. Ventrally segment 6 bears a symmetrical pair of lateral plates, each separated from the tergite by the pleural membrane as is the sternite of the previous segment. Each plate bears macrotrichia which are better developed than those of sternite 5. Were the phylogenetic derivation of *N. magnifica* not reasonably clear, one would probably interpret this structure as the result of median desclerotization of a large, primarily symmetrical sternite 6 resembling the preabdominal sternites (Fig. 6). However, the apparent facts that the *inversa* group is the sister group of the *magnifica* group, that these together form the sister group of the *parviceps* group, and that the three above groups together form the sister group of the *capilo* group, render such an interpretation implausible. The series of protandrograms (Figs 3-6) illustrates the direction of evolution of these structures in the genus *Neurochaeta*. Only the left ventral sclerite of segment 6 in *N. magnifica* can be the homologue of sternite 6, its mirror image on the right side being a secondary sclerite. This condition is somewhat paralleled in *Fannia* (Griffiths, 1972) and *Borboroides* (McAlpine, 1985), where structures present only on the left side in the ancestral form have been mirrored by new structures on the right side, with resultant symmetry. In *N. magnifica*, however, it appears that evolution of segment 6 is in the process of incorporation into the preabdomen, as a continuation of the sclerotization process would restore a full, symmetrical sclerite simulating a typical preabdominal sternite. This kind of process may well be the clue to the possession of an apparent symmetrical, ventral sternite 6 in males of such flies as *Waterhouseia* (family Heleomyzidae, see McAlpine, 1985). It has long appeared to me from study of other families that the groundplan condition of the Schizophora includes strongly asymmetrical protandrial sclerites as in Coelopidae (Crampton, 1942: fig. 12H), and that symmetrical conditions of the protandrium are all secondarily derived. As protandrial morphology has figured prominently in arguments on phylogeny and superfamily classification (see particularly Griffiths, 1972), the correct evolutionary interpretation is important.

Some aspects of the functional changes in the evolution of the neurochaetid protandrium are easily explained. The asymmetry of the sclerites was apparently attained in a remote Mesozoic ancestor through spiral displacement in the process of circumversion of the genital segment (Crampton, 1942). This spiral arrangement of the tergites and sternites in segments 5 to 8 is preserved in modern Coelopidae with almost diagrammatic clarity (Fig. 3). With slight modification, this pattern occurs in the plesiomorphic neurochaetid *Neurochaeta* (*Neurocytta*) *prisca*. *N. prisca* is a relatively large neurochaetid, and size in the groundplan of subgenus *Neurochaeta* had probably been reduced to no more than about 3 mm total length as exemplified by 5 of the 6 known species. Size reduction in flies, as in other animals, is often accompanied by structural simplification, possibly because of ontogenetic difficulties in producing a diversity of structures from small materials, or perhaps mainly because a smaller organism can function on a

simplified plan more readily than can a larger organism. In particular, a smaller body requires less skeletal support. In any case the subgenus *Neurochaeta* has developed a tendency towards symmetry by reduction, *N. capilo* (Fig. 5) and *N. parviceps* showing different stages of this process. Apart from the size reduction-simplification factor, the inherent instability in copulatory structures resulting from speciation processes, considered below, combined with the mechanical requirements of approximate symmetry in flight, are factors which should contribute to development of symmetry. The increase in body size and consequent need for skeletal support, and for a base for additional sensory macrotrichia in *N. magnifica* has resulted in increased ventral sclerotization of segment 6. But in this case there has been no tendency for this reversal of selection pressure to restore the lost asymmetrical sclerites, and resclerotization of the region has produced a new almost symmetrical pattern.

In *N. prisca* the epandrium is well developed and the surstyli are loosely articulated with its margins. In the species of subgenus *Neurochaeta* the surstyli are detached from the reduced epandrium and arise each from its separate basal plate.

The gonites (paired appendages of the hypandrium) consist of a single pair in *N. prisca* and two pairs in subgenus *Neurochaeta*. Like the surstyli they show specific differences in shape.

The aedeagus shows considerable specific variation in length, thickness, and armature in the genus *Neurochaeta*.

Specific differences in male copulatory organs occur in most families of Diptera, sometimes being more remarkable than in the examples cited above, e.g. those in the aedeagus of the heleomyzid genus *Diplogeomyza* (McAlpine, 1967). The Diptera are not peculiar in this respect as such specific characters are so general in insects that taxonomic work on most orders normally takes these characters into account. Probably for insect groups in general it may be stated that the male copulatory organs are more consistently than any other organs the ones which show morphological divergence between closely related species. There is a parallel here with acoustical behaviour, though the latter is probably of less wide occurrence among insects.

Highly specific genitalia characters occur in other groups of animals besides insects. They have been described in many Acari (e.g. Davis, 1968), in Diplopoda (e.g. Johns, 1964), in monogenetic trematodes (Sproston, 1946), in gastropods (e.g. Solem, 1981), in snakes (Dowling and Savage, 1960), in carnivorous marsupials (Woolley, 1982), and in rodents (e.g. Lidicker, 1968). These are probably all cases where there is or has been a possibility of the sexual stages of related species mixing with one another.

There has been difference of opinion as to the reason for specific diversity in the genitalia of insects. Some have held that these specific differences constitute a 'lock and key' isolating mechanism (e.g. Watson, 1966). Mayr (1963: 104), while admitting that mechanical isolation (e.g. by means of genitalia difference) plays 'a very minor role', explains this diversity as neither adaptive nor contributing to isolation, but as a side effect of pleiotropic genes.

SPECIFIC MATING MECHANISMS

Previously (McAlpine, 1969) I have classified specific difference in genitalia as an element of a '*specific mating mechanism*' rather than an isolating mechanism. A specific mating mechanism is defined as any genetically based device which tends to prevent mating or attempted cross-fertilization between species. Common specific mating mechanisms among insects include specific differences in time or place of courtship, differences of courtship pattern, visible appearance, chemical secretion, song, or tactile

recognition marks, and the necessarily correlated specific responses to the stimuli imposed by these.

Specific mating mechanisms have often been classed as 'pre-mating isolating mechanisms' or interpreted as 'reinforcement' of isolation through selection. They are, however, distinct from true isolating mechanisms, in that they are the result of, not necessarily the cause of, some degree of isolation between species, and the 'species isolation concept' is at best a misnomer. Their magnitude, complexity, and intraspecific constancy is only to be explained through their role as specific recognition marks, conditioned through inviability or inferior fitness (including heterozygote disadvantage) of the hybrids which they tend to eliminate. Inferior hybrid fitness is the true cause of isolation (McAlpine, 1969). It is pointed out that even mechanisms of low efficiency can be produced by natural selection, and that in nature hybrids can occur between species having well developed specific mating mechanisms. However, the combined effects of specific mating mechanisms can amount to almost 100% efficiency. Many pairs of species which hybridize readily in the laboratory rarely, if ever do so in nature, even when they are sympatric (Mayr, 1963; Bock, 1984).

In a study of acoustical behaviour in the so-called races of the *Drosophila paulistorum* complex, Bennet-Clark and Ewing (1970) found evidence suggesting that the original barrier to interbreeding is not a difference in song, which is only a secondary mechanism. The fact that sterility barriers are evolving with or even preceding differentiation of song illustrates my point that such specific mating mechanisms are not the real cause of isolation.

The clear distinction between isolation and the specific mating mechanism can be seen in the following example from literature. Fisher (1958) cites recurrent hybrids between the butterflies *Limenitis arthemis* and *L. astyanax* occurring at low frequency in the narrow zone of overlap of these two species. A strong mating preference (specific mating mechanisms on my understanding) is said to be responsible for this low frequency. Apparently the hybrid lineages are eliminated after a few generations because of inferior fitness. If Fisher's data are accurate, the gene pools of the two species are as effectively isolated as if every hybrid zygote perished. He is therefore mistaken in suggesting the populations to be subspecies rather than species. I would agree with Fisher that the 'sexual preference' is favoured by a selective process, but not that this process 'would establish an effective isolation', as effectively complete isolation continues even when the 'sexual preference' breaks down, though with some waste of activity and gametes.

In a reasonably stable population the genes of the overall genotype tend to make up a highly integrated set, and it has long been known that introduction of chromosomal material of one race into that of another can cause significant changes in fitness to the carriers of the mixed genotype (e.g. Dobzhansky and Spassky, 1944). In the case of sympatric interfertile incipient species (which have recently acquired sympatry or are the products of disruptive selection) the hybrid genotypes very generally have inferior fitness to the parental genotypes, or the parental populations will tend to lose their identities. Hence, selection for a specific mating mechanism can occur through interaction with a related species even if the hybrids are viable and fertile.

Thomas (1950) has described the intimate association of the male genital appendages with the vaginal opening of the female during copulation in *Sarcophaga* (Diptera, Sarcophagidae). In this genus the form of the external genitalia shows a high degree of variability which is quite specific, and the female is known to exercise a very precise choice on males attempting to copulate. The conclusion seems inescapable that the pattern of stimulation caused by the structure and perhaps the movements of the male genitalia assist the female to make this choice.

The various male postabdominal organs which show great variation in the genus *Neurochaeta* seem likely to affect the process of copulation in some way, so that a specific response is possible in the female. The large asymmetrically placed sternites 6 and 7 in subgenus *Neurocytta*, absent in subgenus *Neurochaeta*, seem likely to affect the articulation of the genital segment with the preabdomen and thus the mode of wielding the copulatory organs. The paired periphallal appendages, surstyli and gonites, most probably convey tactile stimuli to the female. There can be no doubt that the great difference in length of the aedeagus, together with difference in its cuticular armature between *N. capilo* and *N. parviceps*, enables specific discrimination by females, should any premating behavioural mechanism break down. Though adults of these two species are usually separated by host-plant preference, they can occasionally occur on the same plant.

Despite the views of Eberhard (1985) I find in male genitalia characters some evidence of the geographical character displacement pattern dependent on patterns of sympatry. In the genus *Pseudopomyza* s.l. (Diptera, Pseudopomyzidae) the species occurring in Europe and that in Australia, each widely geographically isolated from others of the genus (probably for a very long period) and not very closely related to each other, have the surstyli essentially similar in shape. In New Zealand, where there are several species which must have evolved with some degree of contact with one another (Harrison, 1959) the surstyli show strong specific differences in shape from those of the above species and from each other. A similar pattern occurs in the genus *Australimyza* (Diptera, Carnidae), where the several New Zealand species have highly specific shapes for the surstyli, but the two species, which are geographically remote from others of the genus, in Australia and Macquarie Island respectively, have similar and relatively simple surstyli. Again, these last two do not appear closely related on the basis of other characters.

In flies of the genus *Euprosopia* and in some other genera of Platystomatidae there is a sclerotized, capsule-like segment of the aedeagus or penis called the glans which is inserted deeply into the female genital tract in copulation. The glans often differs in size between closely related species but is of remarkably constant size within a species, despite great individual variation in body size. In Queensland, the two partially sympatric species *E. separata* and *E. comes* are so similar that females are difficult to distinguish, but males are distinguishable by the size of the glans and some other secondary sexual characters (some information in McAlpine, 1973a). In the more southern part of its range, where it is the only species of its group, *E. comes* apparently has a glans intermediate in size between that of *E. separata* and the more northern populations of *E. comes*. Despite such examples as this I find a detailed uniformity in genitalia characters over a considerable geographic range to be usual in the dipterous groups I have studied.

These data seem to conflict with the pattern given by Eberhard (1985: chapter 3). In some, but not all, of Eberhard's cases the genitalic difference between allopatrics concerns species within genera of considerable specific diversity and the species compared are not necessarily very closely related. Again he may have too readily dismissed the likely significance of unknown historical patterns which could often have been quite complex. The existing allopatry often may be irrelevant to the speciation process. On the other hand some of Eberhard's arguments seem to presuppose that only coexistence of very closely related species can possibly be invoked as producing sexual selection for divergence *per se*, whereas copulations and sometimes hybridism in nature between species of a higher order of differentiation have been observed (e.g. in butterflies and birds).

I summarize my conclusions on specific mating mechanisms (SMMs) in the following 5 statements: —

1. SMMs arise through natural selection acting on sympatric populations of related species.
2. Production of SMMs is not part of the speciation process, though it commonly follows speciation.
3. SMMs reduce wastage of gametes and of time and energy in fruitless reproductive behaviour.
4. SMMs do not (in the long term) prevent introgression (do not cause isolation).
5. SMMs are probably generally maintained by selection.

It is now necessary to consider hypotheses which are not compatible with the SMM viewpoint, but which have arisen partly through some shortcomings of the isolation-reinforcement concept.

H. E. H. Paterson has often stated the view that, while recognition marks are stabilized within a species by natural selection, natural selection has not caused divergence in these characters between related sympatric species (the concept of the specific-mate recognition system or SMRS, see Lambert and Paterson, 1984). According to that viewpoint, divergence in characters involving recognition occurs as a result of random genetic changes in populations of small size before speciation. While the small population model of speciation has become widely accepted, taken alone it is quite incapable of explaining the widespread (in some groups quite general) phenomenon of much greater specific divergence in premating signals than in other characters. Mate recognition would still be an important stabilizing factor at the small population stage, though under reduced mate-choice some slightly deviant phenotypes may be accepted. As with the older speciation model based on geographic variation, an initiation of signal divergence could result, but in my view, there is no reason why, under allopatry, divergence in signal should vastly outstrip divergence in other characters. This final result is clearly directed, not random, and almost certainly depends on sympatry (some examples in genitalia characters given by McAlpine, 1969).

Paterson (1978) supports his view, that the reinforcement model (thus also the specific-mating model) cannot be evolved through interaction between incipient species, by a simple mathematical demonstration. This idea, that, if there is random mating and heterozygote disadvantage in a mixture of two genotypes, the rarer genotype will be so often absorbed into unfit heterozygotes that its extinction is assured, is valid under certain ideal circumstances (experiments of Harper and Lambert, 1983), but let us compare these requirements with the situation in nature.

First, why is it necessary to assume random mating? Paterson accepts that evolution after allopatric separation of a small population makes some divergence in 'SMRS' possible, and thus mating choice in subsequent sympatry need not be entirely random. It has been argued, however, that, where behavioural differences occur, they cannot alone prevent the extinction of one genotype in a closed system. Second, the development of 'reinforcement' or specific mating mechanisms occurs between populations that have diverged to the point of speciation, not between simple mutants of the one population. Third, and perhaps most important, the model depends on a nice mixing under closed conditions of the two genotypes, as in the few laboratory experiments which Paterson considers ideal. In nature the patchiness of the environment renders it more likely that there would be frequent invasion and possibly return between strongholds of the two population types. After each invasion the original occupier would have lost some material from the gene pool, preferentially that most likely to have facilitated cross mating. Any retreating invader would be similarly changed. The very experiments which have been rejected as irrelevant, those in which a mixed culture was artificially maintained, are those most likely to simulate a natural event. It has been pointed out that these laboratory experiments do not result in permanent fixation of

mate recognition systems in the populations, but this is scarcely surprising. The established systems or mechanisms in natural species have often been evolved over many thousands of years, and even then may be imperfect enough to allow occasional hybrids, e.g. in birds of paradise (Gilliard, 1969) and birdwing butterflies (McAlpine, 1970), both groups with obvious specific recognition marks. There is reason to believe that, in sympatric sister species, specific mating mechanisms are maintained by selection, just as they were built up by selection. When changes in the environment bring about breakdown in the true isolating mechanism of hybrid inferiority, the species tend to fuse, because the specific mating mechanism can no longer be maintained (several examples given by Mayr, 1963: chapter 6).

It is not quite reasonable of Lambert and Paterson (1984), whenever there is geographic variation in signal characters, to claim that this variation cannot be in those characteristics of the signal that involve recognition. If the observed variation does not involve recognition marks, why else should it follow the geographic character-displacement pattern observed, for instance, by Littlejohn (1965)? Littlejohn's explanation fits the observed facts, but the SMRS school provides no adequate explanation of observed phenomena. On the other hand, the positive aspect of the SMRS argument does explain the remarkable consistency of specific mating mechanisms within a species, which may extend throughout its geographic range if gene flow permits.

Certainly, some of my above points have been considered by the anti-reinforcement school. For example, Harper and Lambert (1983) consider the effect of continued immigration of one species, but argue that continued gene flow (i.e. introgression) would probably prevent divergence of the populations. As I have previously pointed out, the divergent genomes (under the allopatric speciation model) need to have reached, prior to sympatry, a degree of divergence which ensures that each integrated genome has such superior fitness that hybrid lines are virtually certain to die out in the long term. Populations that have not so diverged are irrelevant to the speciation process, even though they may, if allopatric, be given separate specific names.

Eberhard (1985) discusses Fisher's concept of sexual selection by runaway female choice and favours this explanation for specific divergence in genitalia characters over selection for divergence under at least partial sympatry. Kirkpatrick (1982) has produced a mathematical model for this system. Eberhard argues that the other function of copulation (i.e. other than essential sperm transfer) 'is that of inducing females to receive and use sperm or, in a broad sense, courtship'. The tendency for females to be selective in their sexual partners is a well known corollary of the facts of production of different numbers of gametes and the making of different kinds of investment in the offspring by the two sexes. This principle is also significant in the specific mating mechanism concept. The runaway process can indeed be invoked to explain rapid change in these circumstances, but that the change is under a special kind of control is evidenced by the end result, viz. remarkable uniformity within a species and sharp interspecific difference. These almost universal phenomena do not necessarily arise as the consequence of 'runaway selection' as described particularly by Eberhard. The theoretical aspects of this selection, especially under the explanations given by Eberhard (1985:72), should be a continuing instability and elaboration of detail through female choice favouring novel stimuli. Very generally, such instability does not occur in male genitalia characters. Amazingly, when Eberhard comes to consider intraspecific uniformity of genitalia as a stumbling block to his hypothesis (Eberhard, 1985: 151-153), he finds this evidence 'difficult to evaluate', and then all but denies its existence.

There is also a weakness in the converse side of the runaway female choice argument. Why, if the process takes place quite independently in each species, does it virtually always (in the relevant animal groups) result in strong divergence in genitalic

characters? It might be expected that in the *more complex* systems change *per se* would *usually* result in divergence, but the divergence phenomenon is quite general for various levels of structural complexity.

Some further inconsistencies occur in Eberhard's arguments. He argues (a) that copulation is part of the courtship ritual (b) that copulation is not necessarily the final stage at which female choice can be exerted. (I can agree on both counts.) He then argues that the fact, that the poor correlation of simple, uniform (i.e. non-specific) male genitalia characters with (specific) elaborate premating behaviour, seriously weakens the species isolation hypothesis (presumably meaning for genitalia differences as distinct from courtship differences). As indicated elsewhere, I do not consider any one mechanism to be 100% efficient to the exclusion of other mechanisms; further there is no necessity in any case to believe that the premating mechanism was evolved before the genitalic one, and special problems in gamete wastage will favour reinforcement of recognition mechanisms at all stages in the sexual sequence.

Finally, there are many cases where closely related species do occur sympatrically, are interfertile, and occasionally produce hybrids. The fact that these hybrids (and not the parent species) are eliminated means that 'reinforcement' selection is certainly acting. I find it just about as surprising, then, that some biologists should attempt to disprove the existence of this selection process, as that they should attempt to disprove the existence of upside-down flies.

TAXONOMIC CHARACTERS AND ADAPTATION

The view that genetic changes which result in taxonomic characters are generally differentially adaptive is probably widely accepted. A taxonomic character, if genuine, is generally the phenotypic expression of a number of genes, though it may not represent the whole adaptive expression of any one of its causative genes. The theory of the adaptive nature of taxonomic difference is closely related to the specific niche theory. For both theories, support can be found in many specific examples, but a general proof is not available. Species divergence need not, however, depend on competition.

It is quite possible for taxonomic difference to be adaptive without its bearing on any ecological difference between taxa. Often a taxonomic difference is adaptive to the internal environment of an organism which has itself become modified for various historic and probably adaptive reasons. The difference in chaetotaxy (bristle pattern) between such flies as *Homoneura* (family Lauxaniidae) and *Leucophenga* (family Drosophilidae) may be of this kind. The existing pattern in each group is stable, apparently because it fits the very complex physiology of the organism, although mutations liable to cause different patterns are often produced. Drosophilids manage best without a mesopleural bristle; lauxaniids need a mesopleural bristle (except in the special case of the Celyphinae), though flies of the two groups seem to be performing the same things.

I have consistently sought Darwinian explanations for morphological change and divergence, because no established modern theory has been able to displace 'progressive adaptation' as the driving force in morphological evolution. Neither the theory of molecular drive (Dover, 1982) nor the neutral theory of molecular evolution (outlined by Kumura, 1985) is claimed to have much direct bearing on morphological change, though both are concerned with change at the molecular level. Sometimes, however, hypotheses regarding morphological developments of unknown function are put forward, and there can be a tendency to interpret these under the above categories.

Vines (1982), perhaps finding difficulty in explaining specific differences as the effects of selection, suggests that molecular drive may have an effect 'on any aspect of the

phenotype, from sexual behaviour to morphology'. If this generalization is to be applied to the phenotypes here classed as specific mating mechanisms, then its protagonists must explain the curious coincidence that these phenotypes are always those which have the potential to enable specific discrimination in mating pairs.

Arrow (1951), discussing evolution of enlarged mandibles and horns in Coleoptera, infers a form of evolutionary momentum when he states 'because a process [of evolution] is long continued it is not easily discontinued'. Such ideas have been largely countered by responsible arguments (e.g. Otte and Stayman, 1979; Charlesworth, 1984). Recent interesting studies of evidence for function of diverse developments have included: stalked eyes in Diptera (McAlpine, 1979; Burkhardt and Motte, 1983), horns in Coleoptera (Otte and Stayman, 1979; Eberhard, 1979 — Arrow's problem!); horns in Diptera (Moulds, 1977); diverse secondary sexual developments in Diptera (elements of specific mating mechanisms, McAlpine, 1973b); shell geometry in gastropods (Signor, 1985); coloration in insects (a few examples and references in Matthews, 1976); stripes in zebras (Cloudsley-Thompson, 1984 — involving Diptera!); the tusk in male narwhals (Cetacea) (Gerson and Hickie, 1985). The last example provides support for the analogy I have drawn (McAlpine, 1976) between sinistrally spiral narwhal tusks and sinistrally spiral vibrissae in certain clusiid flies. The examples here quoted can be categorized with most of the morphological types sometimes considered inexplicable in terms of Darwinian selection. The need for alternative theories seems to be disappearing as we take a closer look at organisms in nature.

In the above discussion in general I have been using the term adaptation in virtually a traditional sense, but also in the special sense of Gould and Vrba (1982). That my interpretation of usage of the morphological developments should sometimes extend these characters into the category of exaptation (using the terminology of Gould and Vrba) is for the most part improbable and not intentional. This is because I am considering new developments, which are apomorphies in relation to the groundplan of the Asteioidea and often in relation to that of the Neurochaetidae or even of subgenus *Neurochaeta*. Hence the characters are not likely to be preadapted to uses other than those pertaining to the derived biological pattern of neurochaetids. The possible exception involves the prognathous position of the head in subgenus *Neurochaeta*, which appears to have dual usage in ant mimicry and rear vision. However, there is no reason to assume that prognathy preceded the early stages of either ant mimicry or running backwards and it may be a simultaneous adaptation to two functions.

Attempts by taxonomists to interpret in functional or adaptive terms the characters used in classification are occasionally made, mainly in the more obvious categories, such as specific diversity of bills of birds (examples in Tyne and Berger, 1959). In insects, with the enormous number of taxa and consequently of taxonomic characters, few taxonomists have given time to consider the functional aspects of the characters, and lack of relevant biological data has often placed the problem beyond profitable consideration.

Hlavac (1972) has given a morphological account of the prothorax of Coleoptera, relating the major structural types to locomotory mechanism and habitat adaptation. The differences in structure are to some extent the character differences for major taxa of Coleoptera. He finds that, at somewhat lower taxonomic levels convergence is common 'and putatively unique paradaptive features' are infrequent. This statement recalls the apparent convergence in characters relating to thoracic depression between *Nothoasteia* and the more advanced species of the *Neurochaeta* lineage.

Generation of morpho-adaptive hypotheses for the Neurochaetidae is simpler than for most families of Diptera, because of the small number of taxa, the fairly clear picture

of part of the phylogeny (partly from reference to a key fossil), and some understanding of their biology.

In discussing the morphology of the Neurochaetidae I have produced a series of hypotheses as to adaptive values, which are in accord with the very limited available data on the biology of the insects, or which, considered in relation to one another, make up a plausible picture of aspects of the evolutionary adaptation of neurochaetid flies. In taking my deductions somewhat into the field of speculation I have proceeded further than is usual in the field of insect physiology, but not further than is commonly accepted in the fields of palaeontology and phylogenetic systematics, where elaborate hypotheses are often produced on evidence which is slight or liable to more than one interpretation. As in those fields, I believe that reasonable hypotheses on morphological adaptation in insects are a step towards a more complete understanding of a little investigated but highly complex subject, and provide some indications for the direction of future work.

ACKNOWLEDGEMENTS

I am indebted to W. D. Hamilton, R. W. Taylor and D. J. Bickel for discussion of some of the ideas here put forward. K. C. Khoo assisted in field observations, B. Duckworth assisted with the illustrations, and J. Howarth processed the words.

References

- ARROW, G. J., 1951. — *Horned beetles, a study of the fantastic in nature*. The Hague: W. Junk.
- BENNET-CLARK, H. C., and EWING, A. W., 1970. — The love song of the fruit fly. *Scientific Amer.* 223: 84-92.
- BOCK, I. R., 1984. — Interspecific hybridization in the genus *Drosophila*. *Evol. Biol.* 18: 41-70.
- BOONSONG, L., and MCNEELY, J. A., 1977. — *Mammals of Thailand*. Bangkok: Kurusapha Ladprao Press.
- BURKHARDT, D., and MOTTE, I. DE LA, 1983. — How stalk-eyed flies eye stalk-eyed flies: observations and measurements of the eyes of *Cyrtodiopsis whitei* (Diopsidae, Diptera). *J. Comp. Physiol.* 151: 407-421.
- CHARLESWORTH, B., 1984. — Evolution of the giraffe's neck. *New Scient.* 1426: 59-61.
- CLOUDSLEY-THOMPSON, J. L., 1984. — How the zebra got his stripes — new solutions to an old problem. *Biologist* 31: 226-228.
- COLLESS, D. H., and MCALPINE, D. K., 1970. — Chapter 34. Diptera. In *The insects of Australia*: 656-740. Melbourne: Melbourne University Press.
- CRAMPTON, G. C., 1942. — The external morphology of the Diptera. *Bull. Conn. geol. nat. Hist. Surv.* 64: 10-165.
- DAVIS, J. J., 1968. — Studies in Queensland Tetranychidae. 7. Records of the genus *Eotetranychus* (Acarina: Tetranychidae). *J. Aust. ent. Soc.* 7: 127-129.
- DOBZHANSKY, T., and SPASSKY, B., 1944. — Genetics of natural populations. XI. Manifestation of genetic variants in *Drosophila pseudoobscura* in different environments. *Genetics* 20: 270-290.
- DOVER, G., 1982. — Molecular drive: a cohesive mode of species evolution. *Nature* 299: 111-117.
- DOWLING, H. G., and SAVAGE, J. M., 1960. — A guide to the snake hemipenis: a survey of basic structure and systematic characteristics. *Zoologica* 45: 17-28, 3 pl.
- EBERHARD, W. G., 1979. — The function of horns in *Podischnus agenor* (Dynastinae) and other beetles. In M. S. and N. A. BLUM, (eds), *Sexual selection and reproductive competition in insects*: 231-258. New York: Academic Press.
- , 1985. — *Sexual selection and animal genitalia*. Cambridge, Mass: Harvard University Press.
- FISHER, R. A., 1958. — *Genetical theory of natural selection*. 2nd edition. New York: Dover.
- GERSON, H. B., and HICKIE, J. P., 1985. — Head scarring on male narwhals (*Monodon monoceros*); evidence for aggressive tusk use. *Can. J. Zool.* 63: 2083-2087.
- GILLIARD, E. T., 1969. — *Birds of paradise and bower birds*. London: Weidenfeld and Nicolson.
- GOULD, S. J., and VRBA, E. S., 1982. — Exaptation — a missing term in the science of form. *Paleobiol.* 8: 4-15.
- GRIFFITHS, G. C. D., 1972. — *The phylogenetic classification of Diptera Schizophora with special reference to the structure of the male postabdomen*. Hague: W. Junk.
- HARPER, A. A., and LAMBERT, D. M., 1983. — The population genetics of reinforcing selection. *Genetica* 62: 15-23.
- HENNIG, W., 1965. — Die Acalyptratae des Baltischen Bernsteins und ihre Bedeutung für die Erforschung der phylogenetischen Entwicklung dieser Diptera-Gruppe. *Stuttgart. Beitr. Naturk.* 145: 215 pp.
- HLAVAC, T. J., 1972. — The prothorax of Coleoptera: origin, major features of variation. *Psyche* 79: 123-149.

- JOHNS, P. M., 1964. — The Sphaerotrachopidae (Diplopoda) of New Zealand. 1. Introduction, revision of some known species and descriptions of new species. *Rec. Canterbury (N.Z.) Mus.* 8: 1-49.
- KIMURA, M., 1985. — The neutral theory of molecular evolution. *New Scient.* 1464: 41-46.
- KIRKPATRICK, M., 1982. — Sexual selection and the evolution of female choice. *Evolution* 36: 1-12.
- LAMBERT, D. M., and PATERSON, H. E. H., 1984. — On 'bridging the gap between race and species': the isolation concept and an alternative. *Proc. Linn. Soc. N.S.W.* 107: 501-514.
- LIDICKER, W. Z., 1968. — A phylogeny of New Guinea rodent genera based on phallic morphology. *J. Mammal.* 49: 609-643.
- LITTLEJOHN, M. J., 1965. — Premating isolation in the *Hyla ewingi* complex (Anura: Hylidae). *Evolution* 19: 234-243.
- MCALPINE, D. K., 1967. — The Australian species of *Diplogeomyza* and allied genera (Diptera, Heleomyzidae). *Proc. Linn. Soc. N.S.W.* 92: 74-106.
- , 1969. — Systematic studies in Australian Platystomatidae (Diptera). London: University of London, Ph.D. thesis, unpubl.
- , 1970. — A note on the status of *Ornithoptera allottii* (Rothschild) (Lepidoptera: Papilionidae). *J. Aust. ent. Soc.* 9: 233-234.
- , 1973a. — The Australian Platystomatidae (Diptera, Schizophora) with a revision of five genera. *Mem. Aust. Mus.* 15: 256 pp.
- , 1973b. — Observations on sexual behaviour in some Australian Platystomatidae (Diptera, Schizophora). *Rec. Aust. Mus.* 29: 1-10.
- , 1976. — Spiral vibrissae in some clusiid flies (Diptera, Schizophora). *Aust. ent. Mag.* 3: 75-78.
- , 1978. — Description and biology of a new genus of flies representing a new family (Diptera, Schizophora, Neurochaetidae). *Ann. Natal Mus.* 23: 273-295.
- , 1979. — Agonistic behaviour in *Achias australis* (Diptera, Platystomatidae) and the significance of eye-stalks. In M. S. and N. A. BLUM, (eds) *Sexual selection and reproductive competition in insects*: 221-230. New York: Academic Press.
- , 1983. — A new subfamily of Aulacigastridae (Diptera: Schizophora), with a discussion of aulacigastrid classification. *Aust. J. Zool.* 31: 55-78.
- , 1985. — The Australian genera of Heleomyzidae (Diptera: Schizophora) and a reclassification of the family into tribes. *Rec. Aust. Mus.* 36: 203-251.
- , 1988. — Studies in upside-down flies (Diptera: Neurochaetidae). Part I. Systematics and phylogeny. *Proc. Linn. Soc. N.S.W.* 110: 31-58.
- MATTHEWS, E. G., 1976. — *Insect ecology*. St Lucia, Qd: University of Queensland Press.
- MAYR, E., 1963. — *Animal species and evolution*. Cambridge, Mass: Harvard University Press.
- MOULDS, M. S., 1977. — Field observations on behaviour of a north Queensland species of *Phytalmia* (Diptera: Tephritidae). *J. Aust. ent. Soc.* 16: 347-352.
- OTTE, D., and STAYMAN, K., 1979. — Beetle horns: some patterns of functional morphology. In M. S. and N. A. BLUM, eds, *Sexual selection and reproductive competition in insects*: 259-292. New York: Academic Press.
- PATERSON, H. E. H., 1978. — More evidence against speciation by reinforcement. *S. Afr. J. Sci.* 74: 369-371.
- SHAW, D. E., and CANTRELL, B. K., 1983. — Further notes on seed set in *Alocasia macrorrhiza* (Araceae) and occurrence of *Neurochaeta inversa* (Diptera: Neurochaetidae) in Queensland. *Qd Nat.* 24: 71-75.
- , —, and HOUSTON, K. J., 1982. — *Neurochaeta inversa* McAlpine (Diptera: Neurochaetidae) and seed set in *Alocasia macrorrhiza* (L.) G. Don (Araceae) in southeast Queensland. *Proc. Linn. Soc. N.S.W.* 106: 67-82.
- SIGNOR, P. W., 1985. — The role of shell geometry as a deterrent to predation in terebrid gastropods. *Sci. in N. Guinea* 11: 81-95.
- SOLEM, A., 1981. — Camaenid land snails from Western and Central Australia (Mollusca: Pulmonata: Camaenidae). 11. Taxa from the Kimberley, *Amplirhagada* Iredale, 1933. *Rec. West. Aust. Mus. Suppl.* 11: 147-320.
- SPROSTON, N. G., 1946. — A synopsis of the monogenetic trematodes. *Trans zool. Soc. London* 25: 185-600.
- STONE, B. C., 1982. — New Guinea Pandanaceae: first approach to ecology and biogeography. In J. L. GRESSITT, (ed.), *Biogeography and ecology of New Guinea* 1: 401-436.
- THOMAS, H. T., 1950. — Field notes on the mating habits of *Sarcophaga* Meigen (Diptera). *Proc. Roy. ent. Soc. (A)* 25: 93-98.
- TYNE, J. VAN, and BERGER, A. J., 1959. — *Fundamentals of ornithology*. New York: John Wiley and Sons.
- VINES, G., 1982. — Molecular drive: a third force in evolution. *New Scient.* 96: 664-665.
- WATSON, J. A. L., 1966. — Genital structure as an isolating mechanism in Odonata. *Proc. Roy. ent. soc. Lond. (A)* 41: 171-174.
- WICKLER, W., 1968. — *Mimicry in plants and animals*. New York: McGraw-Hill.
- WOODLEY, N. E. 1982. — Two new species of *Neurochaeta* McAlpine (Diptera: Neurochaetidae), with notes on cladistic relationships within the genus. *Mem. ent. Soc. Wash.* 10: 211-218.

- WOOLLEY, P. A. 1982. — Phallic morphology of the Australian species of *Antechinus* (Dasyuridae, Marsupialia): a new taxonomic tool? In M. ARCHER, (ed.), *Carnivorous marsupials* 2: 767-781. Sydney: Royal Zoological Society of N.S.W.